OBSERVATIONS OF WOOD THRUSH NEST PREDATORS IN A LARGE CONTIGUOUS FOREST

GEORGE L. FARNSWORTH¹ AND THEODORE R. SIMONS^{1,2}

ABSTRACT.—We used inexpensive (<\$30) cameras to document predators at active Wood Thrush (*Hylocichla mustelina*) nests in Great Smoky Mountains National Park. We observed such predators as black rat snakes (*Elaphe obsoleta*), American Crows (*Corvus brachyrhynchos*), southern flying squirrels (*Glaucomys volans*), and black bears (*Ursus americanus*) remove the contents of nests. Camera installation had no measurable effect on nest survival; daily nest survival was approximately 0.96 for nests with and without cameras. However, placement of an artificial egg trigger in the nest appeared to reduce hatching success. The immobile egg trigger might have interfered with the female Wood Thrush's ability to incubate her eggs. The variety of nest predators observed and the moderate daily survival rates recorded suggest that predation is an important constraint on Wood Thrushes nesting in large contiguous forests. *Received 18 March 1999, accepted 25 August 1999*.

The primary cause of nest failure among forest nesting passerines is predation (Ricklefs 1969, Martin 1993). The prevailing fragmentation hypothesis suggests that predation rates are higher in fragmented landscapes than in contiguous forest (Robinson et al. 1995). This pattern has been demonstrated for several species of Neotropical migrants, including Wood Thrushes (Hylocichla mustelina) whose populations have experienced consistent declines in recent years (Robbins et al. 1989, Peterjohn et al. 1995). Studies in small to moderate sized forest fragments consistently have shown an inverse relationship between forest patch size and nest predation rates (Wilcove 1985, Donovan et al. 1995, Hoover et al. 1995, Robinson et al. 1995, Weinberg and Roth 1998). In contrast, data from 416 nests monitored over five breeding seasons in Great Smoky Mountains National Park suggest that the inverse relationship between forest patch size and nest predation rates may disappear or even reverse when habitat patches exceed size or disturbance thresholds (Farnsworth 1998, Farnsworth and Simons 1999). Average daily nest survival rates in the park (the largest contiguous tract of forest in the eastern U.S.) were substantially less than those reported in studies on moderately large forest tracts (Farnsworth and Simons 1999). These findings suggest that while daily nest survival rates may increase with forest patch size at intermediate spatial scales, they may level off or even decline in very large and protected patches, resulting in what Suarez and coworkers (1993) have called the "paradox of predation."

Although it is generally agreed that predation is an important influence on forest songbird populations, it is surprising how little direct evidence is available about nest predators. Many authors have listed potential songbird nest predators, including American Crows (Corvus brachyrhynchos), Blue Jays (Cyanocitta cristata), raccoons (Procyon lotor), squirrels, and snakes (see Martin 1988, Yahner and DeLong 1992, Roth et al. 1996). Other authors have attempted to attribute nest failures to predators based on eggshell remains in the nest and nest disturbance (e.g., Johnson 1979, Moors 1983). However, when Marini and Melo (1998) presented captive predators (reptiles, birds, and mammals) with eggs, they found that eggshell remains were not diagnostic of the predator involved. This result casts doubt on studies that use nest remains to categorize predators. Interestingly, none of the 86 snakes (comprising 22 species) tested by Marini and Melo consumed eggs in captivity. Roper and Goldstein (1997) obtained a similar result. They tested 12 genera of snakes and found only one genus, Pseustes, that ate eggs in captivity.

Some researchers have used cameras at artificial nests to document potential predators (e.g., Laurance and Grant 1994, Picman and Schriml 1994, Danielson et al. 1996). However predators of artificial nests may not be the same as those of active nests (Major and Kendal 1996). Few studies have been able to

¹Cooperative Fish and Wildlife Research Unit, Dept. of Zoology, North Carolina State Univ., Raleigh, NC 27695.

² Corresponding author; E-mail: tsimons@nesu.edu

identify the predators at natural nests. Some have been able to document predators at active nests using expensive time-lapse video or movie cameras (e.g., Henson and Grant 1992, Booth et al. 1996, Brown et al. 1998, Thompson et al. 1999). While these systems can be effective, their cost generally limits their application to a small number of nests. A notable exception is the study by Major and Growing (1994), which identified predators at New Holland Honeyeater (Phylidonyris novaehollandiae) nests. They used inexpensive automated cameras to photograph nests at the moment the contents were being eaten. They identified the primary predator as black rats (Rattus rattus).

In this paper, we present results obtained from an inexpensive camera system developed to identify the predators at Wood Thrush nests in Great Smoky Mountains National Park. Understanding the relative importance of the predators responsible for nest failures in this relatively pristine habitat may shed light on the relatively low daily nest survival rates recorded in the park and may provide a baseline for comparisons to studies on more fragmented landscapes.

STUDY AREA AND METHODS

Great Smoky Mountains National Park straddles the border of North Carolina and Tennessee, encompassing an elevation range from 300-2020 m. Since its establishment as a National Park in 1934, all logging has been prohibited and forest fires have been controlled, creating one of the largest contiguous tracts of forest (202,000 ha) in the eastern U.S. We located and monitored Wood Thrush nests in the park from 1995 to 1997 as part of a larger study (Farnsworth 1998, Farnsworth and Simons 1999). Once located, nests were visited once every three days. We placed eameras to doeument nest predators during three breeding seasons. Not all nests we found were suitable for camera installation. Therefore the sample of nests at which we installed cameras was not random. We were restricted to installing cameras at nests low enough to allow us access with a 1.8 m (6 ft) ladder.

Camera units consisted of an inexpensive fixed focus camera (\$5.00; model AK41ZL promotional 35 mm camera from Two Jays Inc., Mount Holly, New Jersey) housed within a plastic food container painted green (Fig. 1). The camera was triggered by an egg placed in the nest (alongside the natural eggs in active nests or as a single egg in a recently depredated nest) and tethered to a relay by a short section of monofilament (40 lb. test). We used a Northern Bobwhite (*Colinus virginianus*) egg with a mechanical relay in 1995, and a painted wooden egg with an electronie

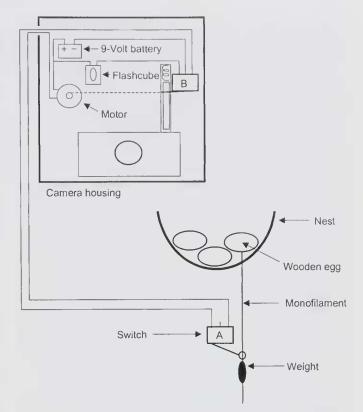


FIG. 1. Schematic of nest monitoring camera and egg trigger. When the wooden egg was lifted, switch A closed the circuit from the battery to the motor. The motor pulled a string (dotted line) attached to a pin (not pictured). Removal of the pin released a springloaded dowel and activated switch B. Switch B closed the circuit from the battery to the flashcube and opened the circuit from the battery to the motor. The dowel then depressed the shutter release on the camera taking a picture.

relay in 1996 and 1997. The electronic relay was far more reliable and consisted of a submini lever switch (Catalog part # 275-016A; Radio Shack) mounted on the trunk or a horizontal branch below the nest. The monofilament was threaded through an eye-hook glued to the lever switch. A fishing weight was attached to the monofilament below the eye-hook. The switch was connected to the camera housing via 22 guage electrical wires (approximately 7 m in length). The camera housing contained a 9 volt battery forming two cireuits, one to the motor (Catalog part # 273-223; Radio Shaek) and one to the flashcube. When the trigger egg was lifted, switch A (Fig. 1) closed the circuit with the motor. The motor pulled a pin that was holding a spring-loaded dowel. The dowel was held in a PVC pipe with a notch cut into it. The pin prevented the dowel from depressing the shutter-release button on the camera. Removal of the pin also activated a second submini lever switch. Activating this switch simultaneously turned off the motor and sent current to the flasheube. It was necessary to activate the flasheube before depressing the shutter-release button because approximately 10 milliseconds were required to illuminate the flashcube. Once a flash picture was taken, there was no further drain on the battery because all circuits were open. Therefore the total battery usage with this system was minimal (< 1 sec per photograph), and a camera unit could remain operational for several weeks. We mounted cameras at least 1 m from nests (usually on a nearby tree), and in most cases could complete an installation in 5 min. The cost of all materials was approximately \$30.00 per unit.

To examine the effect of the disturbance caused by installing cameras, we compared the daily survival rate (Mayfield 1975) of nests with cameras to the daily survival rate of nests without cameras using a z-test (Johnson 1979). We compared the hatching rate of eggs in nests with and without cameras installed. It usually takes 2 days for all the eggs in a clutch to hatch (Roth et al. 1996). Therefore, only nests observed initially with eggs and later with chicks at least 3 days old were included in this analysis. Eggs found in nests with chicks 3 days old or older were considered to have failed to hatch. We used a G-test of independence to test if the hatching rate of eggs was independent of the presence of a trigger egg in the nest. Because the hatching of each egg within a clutch is not independent, we compared the proportion of camera and noncamera nests in which at least one egg failed to hatch using a G-test of independence. All statistical tests were performed with SAS (version 7) under Windows NT 4.0.

RESULTS

We installed camera units at 57 active Wood Thrush nests. Eleven of these nests were apparently abandoned immediately, and two other nests were initially accepted but abandoned a few days after installation. The camera unit was triggered by the attending Wood Thrush on three occasions. Seventeen nests eventually fledged young. Nineteen cameras were installed on nests after a predator had already visited an active nest (four nests belonged to both groups). The camera unit failed to take a picture when the contents of the nest were disturbed or removed on 18 occasions. A photograph was recovered but no predator was visible on 11 occasions.

We documented eight different species of predators removing eggs from active or recently depredated Wood Thrush nests. Of 19 photographs taken of predators, 7 were records of predation at active nests, and 12 were records of predators at recently depredated nests. At active nests we obtained two pictures each of American Crows (*Corvus brachyrhynchos*), black rat snakes (*Elaphe obsoleta*), and black bears (*Ursus americanus*) and one picture of an Eastern Screech-Owl (*Otus asio*). Three of these photographs (one each of American Crow, black bear, and Screech-owl) were taken at nests with Wood Thrush chicks, the remainder at nests with eggs. In addition to the photographs, we have good evidence of bear predation from two other nests. In these cases nest trees were found clawed and bent over, and the nests were destroyed.

The 12 pictures from recently depredated nests included 5 crows, 3 southern flying squirrels (*Glaucomys volans*), a black rat snake, least weasel (*Mustela rixosa*), whitefooted mouse (*Peromyscus leucopus*), and gray squirrel (*Sciurus carolinensis*). Three of the crow pictures were obtained from the same nest (after first recording a flying squirrel) and the other was from one of the active nests described above.

We compared the nesting success of nests with camera units installed to nests without camera units. There were 3167.5 exposure days and 136 failures at nests without cameras (285 nests) and 604 nest exposure days and 25 failures where cameras were installed and accepted (46 nests). The resulting daily survival rate estimates, 0.957 [\pm 0.004 (SE)] for nests without cameras and 0.959 (\pm 0.008) for nests with cameras, were not different (z =0.17, P > 0.05).

Cameras were accepted by incubating adults at 45 nests and 24 (53%) of these nests survived to hatching as defined above. The average number of days of incubation between camera installation and hatching was 9.7 days. Hatching success at nests without cameras was 0.949 (332 of 350 eggs hatched). At nests with cameras, eggs hatched at a rate of only 0.869 (73 chicks hatched from 84 eggs). The reduction in hatching probability was significant (*G*-test of independence: G_{adj} = 5.67, 1 df; P = 0.017). Fifteen of 100 control nests had at least one unhatched egg, and 10 of 24 nests with cameras failed to hatch at least one egg ($G_{adi} = 7.24$, 1 df; P < 0.01).

The amount of time between camera installation and hatching did not appear to affect the probability of hatching. We divided nests with cameras into two groups, those at which incubation continued for fewer than 10 days before hatching and those incubated for more than 10 days. Hatching rates in the two groups were nearly identical (0.870 vs 0.868 respectively; $G_{adj} < 0.01$, 1 df; P > 0.05).

DISCUSSION

We are encouraged that a simple inexpensive camera system can provide new insights into the causes of forest songbird nest predation. An artificial egg trigger added to an active nest appears to be effective for documenting a variety of nest predators during both the incubation and the nestling stages. The daily survival rates of nests with cameras were no different from nests without cameras suggesting that the effect of the cameras on the nesting birds is minimal.

We made substantial improvements to the cameras during the study; however, more improvement is possible. In 1996 a number of cameras failed when the switch below the nest (switch A; Fig. 1) got wet and shorted the battery. Waterproofing the switch resolved the problem. Because we did not want to alter the visibility of nests by removing vegetation, it was difficult in many situations to mount the camera with a clear line of sight to the nest. As a result 11 pictures were taken at depredated nests but no evidence of a predator could be found on the photograph.

Addition of a tethered egg to the clutch may have caused nest abandonment and reduced hatching success in some nests. The tethered egg triggers were fixed to a piece of stiff monofilament that kept the egg from moving in the nest. On one occasion, we installed a camera at a nest on 3 June 1997 and on 6 June, the nest was discovered to be abandoned and the wooden egg had been damaged, suggesting the Wood Thrush returned to the nest and attempted to remove the wooden egg. The trigger egg may also have inhibited the female's ability to turn the other eggs in the clutch and may have reduced hatching success. Periodic rotation of eggs during incubation is necessary to ensure proper development of the embryo (Drent 1975). A more flexible egg trigger (perhaps incorporating a proximity switch instead of a tether) may more closely mimic a real egg, making it more likely to be accepted and less likely to reduce hatching success.

We were not able to place cameras at all nests discovered. Many nests were too close to heavily used hiking trails, other nests were too high for us to reach, even with a ladder. Therefore our results may represent an incomplete or biased sample of Wood Thrush nest predators on our study sites. The camera system described here could probably be successfully adapted for use on ground or low shrub nesting species such as Ovenbirds (*Seiurus aurocapillus*) and Hooded Warblers (*Wilsonia citrina*). We successfully installed cameras at nests of both of these species during our study.

Another potential bias associated with using automated cameras is that cameras may attract predators. Although we found no increase in predation rates at nests with cameras compared to nests without cameras, we do not know if the predators at these two types of nests were similar. Predators may also learn to associate cameras with a reward of eggs. Among the photographs taken at active nests, no two pictures of the same predator species were taken within 30 km of each other, suggesting that we did not observe an individual predator learning to associate cameras with eggs. We did record the same species (presumably the same individual) up to three times at the same nest.

In light of recent studies with captive snakes (Roper and Goldstein 1997, Marini and Melo 1998), it is noteworthy that we photographed a black rat snake removing a quail egg from a nest that had failed a few days earlier. The egg was at ambient temperature, suggesting that the snake may have been returning to a nest it had discovered previously. Similar observations were made of crows and flying squirrels returning to recently depredated nests. Installing cameras at nests after they fail may be an effective and less intrusive technique for documenting nest predators.

This work is a small step toward developing better techniques for understanding the effects of predation on Wood Thrush and other forest songbirds. We found a diversity of predators responsible for the relatively high rate of Wood Thrush nest failures in Great Smoky Mountains National Park. The park, a large and relatively undisturbed protected area within a largely forested Southern Appalachians landscape, represents a relatively pristine habitat where the effects of forest fragmentation on natural communities should be minimal. Similar studies conducted in other large forests as well as small and medium-sized forest fragments, are necessary to understand how nest predation varies with landscape composition and land use.

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